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THE ASSORTMENT OF CHROMOSOMES IN TRIPLOID DATURAS

JOHN BELLING AND ALBERT F. BLAKESLEE

STATION FOR EXPERIMENTAL EVOLUTION, COLD SPRING HARBOR, LONG ISLAND, NEW YORK

The present article is the one of a number of proposed papers which will deal with the behavior of the chromosomes in the different classes of Datura mutants, the correlation of the chromosomal differences with changes in structural and other characters, and with the ratios in which Mendelian allelomorphs are found in the offspring. The method mainly used in the microscopical examination, and the general principles involved, are given in two papers already in press for THE AMERICAN NATURALIST.

Sizes of Chromosomes.—The diploid *Datura Stra-*

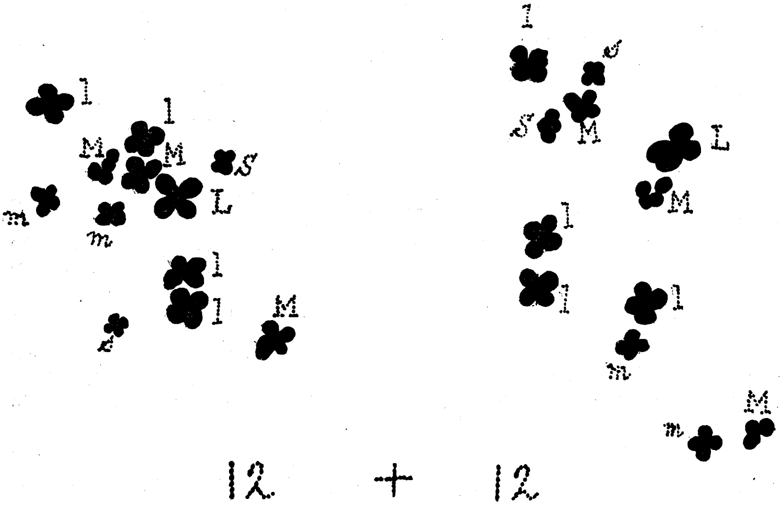
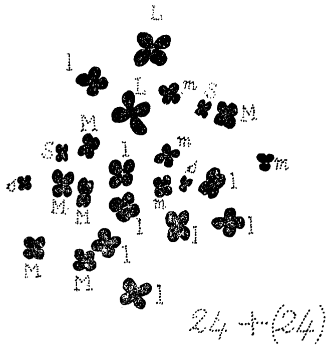
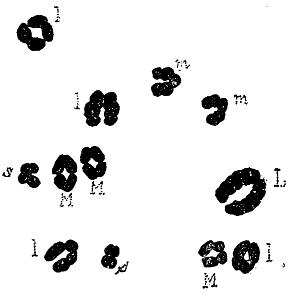
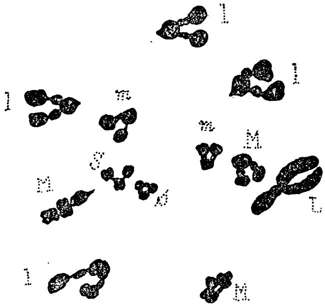


FIG. 1. Second metaphases of a normal Datura in a pollen-mother-cell. The chromosomes are about to divide into two, and each half is constricted. (This figure, as well as Figs. 2 to 6, is a camera drawing of a preparation in iron-aceto-carmine, the cytoplasm having been thinned and flattened by appropriate pressure so that the chromosomes were in optical contact with the cover-glass.)

monium shows, in the metaphase of the second division in the pollen-mother-cells (Fig. 1), two groups, each consisting of 1 extra large chromosome, 4 large, 3 large medium, and 2 small medium chromosomes, 1 small and 1 extra small chromosome. Thus the somatic formula is $2(L + 4l + 3M + 2m + S + s)$. Tetraploid plants have arisen, in rare cases, from these diploid Daturas (2). They show (Fig. 2) twice as many chromosomes in each of the size classes, and have the somatic formula $4(L + 4l + 3M + 2m + S + s)$. Out of many crosses of tetraploid







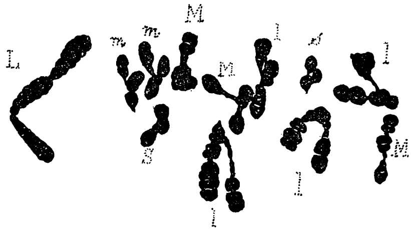


FIG. 2. One second metaphase plate of a tetraploid Datura, in a pollen-mother-cell.

FIG. 3. Late prophase of a normal Datura in a pollen-mother-cell. The size differences are especially distinct, for the smaller chromosomes have condensed earlier.

FIG. 4. Late prophase of a triploid Datura. The largest chromosome set (trivalent) was the latest to condense.

FIG. 5. Late prophase of a triploid Datura. The largest chromosome set is hook-shaped. (The late prophase or early metaphase trivalents often have the form of a ring with a handle, which is indicated in only one trivalent in Fig 4, and is not shown in Fig. 5.)

Daturas by pollen from normals, 4 triploid plants have resulted (3). Their somatic formula is shown to be 3(L + 4l + 3M + 2m + S + s). Similar results have been obtained for triploid hyacinths by de Mol (7).

Attraction of Homologous Chromosomes.—In the normal Daturas the late prophase or early metaphase of the first division in the pollen-mother-cells shows 12 sets with two united chromosomes (bivalents) in each (Fig. 3). These bivalents can readily be arranged in the six size classes. In the corresponding stage of the triploid Daturas there are 12 sets of three united chromosomes each, and these trivalents can be arranged according to the size formula (Fig. 4). Sometimes two of the three rod-shaped chromosomes are united together at both ends, and the third is joined on at one end only, or the three may form a hook (Fig. 5). Some trivalents were seen by Osawa in triploid mulberries (8), and a group of 9 trivalents was also found in a triploid Canna (1). (The complete group of 9 trivalents has also been seen in 4 other triploid Cannas.)

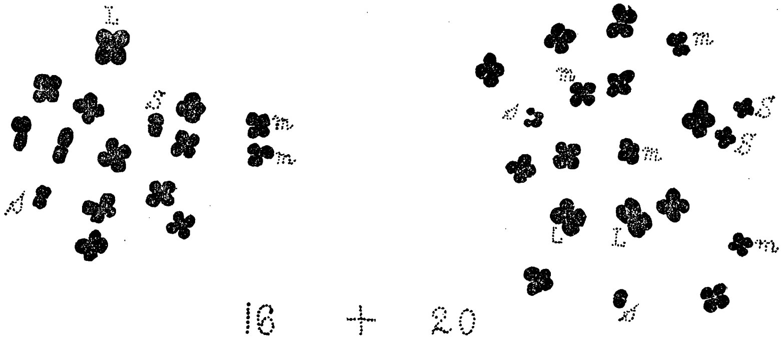


Fig. 6. Second metaphases in a pollen-mother-cell of a triploid Datura. The large and large medium chromosomes were not separable in this preparation.

Separation (Disjunction) of Chromosomes.—So far as seen in Datura, two chromosomes usually pass to one pole, and one chromosome to the other, from each trivalent, as is the case in triploid Cannas (1).

Assortment of Chromosomes.—From one triploid plant both groups of chromosomes were counted in each of 84 pollen-mother-cells, which were in the second metaphases, and showed no detached chromosomes (Fig. 6). The assortments are given in Table I.

TABLE I

ASSORTMENT OF CHROMOSOMES IN 84 POLLEN-MOTHER CELLS OF TRIPLOID DATURA, 19729(1)

Metaphase of Second Division

Assortment of Chromosomes	12 + 24	13 + 23	14 + 22	15 + 21	16 + 20	17 + 19	18 + 18
Nos. of double groups	1	1	6	13	17	26	20
Calculated on random orientation of trivalents	0.04	0.5	2.7	9.0	20.3	32.5	19.0

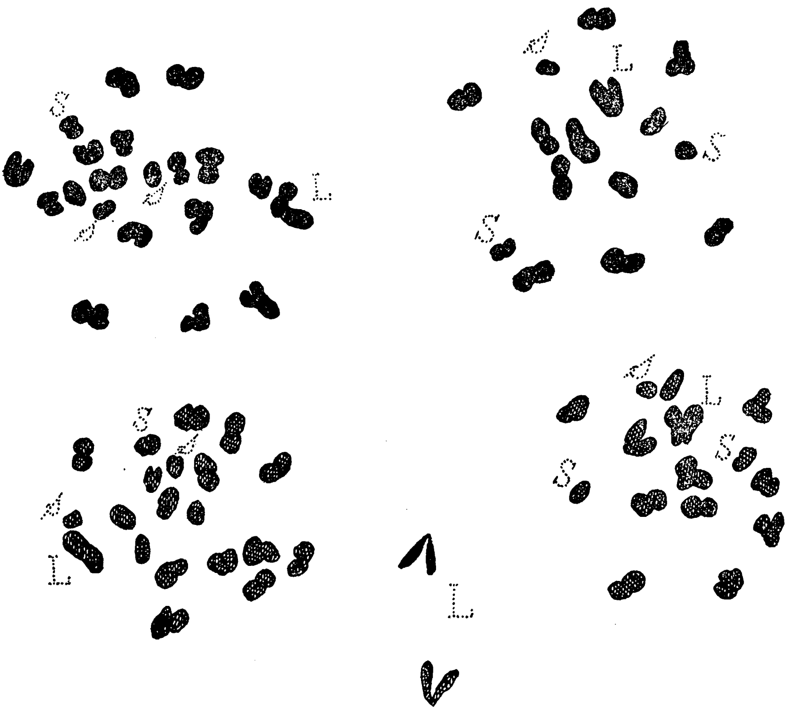


FIG. 7. Early anaphase of the second division in a pollen-mother-cell of a triploid Datura. (The upper right-hand plate was shifted upwards in drawing.) One of the 3 extra large chromosomes had apparently been detached at the first anaphase, and divided at the second division. Probably a tetrad with 2 microcytes would have resulted.

It is evident that the orientation of the trivalents in the first metaphase must be nearly or quite a random one, as was suggested in triploid Œnotheras (5, 6) and mulberries (8), and as is the case in triploid Cannas (1). (Nearly similar results were also obtained from a total of 58 single-metaphase plates from this triploid Datura.)

Detachment of Chromosomes.—Three buds yielded 62 pollen-mother-cells with both second-metaphase plates countable, and among these there were six cells showing that one chromosome had been detached at the first anaphase (Fig. 7), one cell showing detachment of two chromosomes, and one cell showing both one and two detached chromosomes. Thus there were about 13 per cent. of cases of detachment. These detached chromosomes (8) form microcytes when the pollen-mother-cells constrict to form tetrads (Fig. 8). Table II shows the numbers of microcytes seen in nearly 3,500 tetrads from 3 triploid plants. The average is 13 per cent. of cases of detachment, but the variation in different buds appears too great to be due to chance alone. In 100 pollen-grains there would be about 5 microcytes.

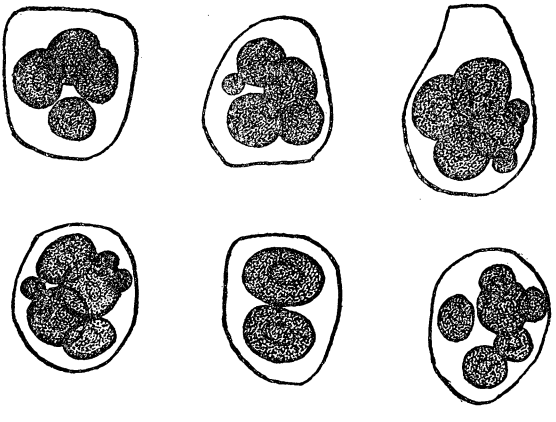


FIG. 8. Tetrads, etc., of a triploid Datura. Above: (1) a normal tetrad; (2) a tetrad with one microcyte; (3) a tetrad with 2 microcytes. Below: (1) a tetrad with 4 microcytes; (2) two giant cells; (3) rare form with 6 not very unequal cells.

Non-reduction.—In belated pollen-mother-cells the chromosomes in the trivalents assume the four-lobed condition of those in the adjoining cells which are in the metaphase of the second division. The first nuclear division is entirely omitted, there is no reduction (8), and two nuclei with 36 chromosomes each are formed at the second division. The two cells which result are twice the size of the average microspores, and can be seen in the pollen as giant grains. Non-reduction may be greatly increased by transient cold. It averaged 0.4 per cent. in the tetrads. A hundred full pollen-grains were measured at random from each of 8 flowers on 4 triploid plants. The average was 0.5 per cent. of giant grains.

TABLE II

DETACHMENT OF CHROMOSOMES. NON-REDUCTION

Pollen Tetrads of Triploid Plants. (Percentages)

	Regular Microspores					Double-sized Microspores					
Nos. of Microspores	4	4	4	4	4	2	2	2	Etc.	Percentage of Cases of Detachment	Nos. of Tetrads
Nos. of Microcytes	—	1	2	3	4	—	1	2			
Plant and Bud											
19729 (1) *a*	67.0	20.0	9.0	0.7	0.5	2.0	0.5	0.2		30.9	403
19729 (1) *b*	91.5	3.0	5.3	0.2						8.5	436
19729 (1) *c*	90.3	3.3	5.9	0.2	0.2					9.6	425
19729 (1) *d*	96.1	1.6	0.9	—	—	1.4				2.5	433
20345 (1) *a*	83.8	7.9	8.1	0.2						16.2	444
20345 (1) *b*	97.8	0.5	0.7	—	—	0.7			0.2	1.2	412
20345 (1) *c*	98.0	0.8	0.3	—	—	1.0				1.1	400
20380 (1) –	65.5	19.0	14.6	—	—	0.6	—	0.4		34.0	542
Average	86.3	7.0	5.6	0.2	0.1	0.7	0.1	0.1	0.03	13.0	Total 3,495
Microcytes to 100 pollen-grains = 4.9						Percentage of double-sized pollen-grains = 0.4					

Chromosomes of Functional Egg-cells.—In one triploid Datura, from three (or fewer) capsules pollinated by a normal, there were produced 75 mature plants, 67 of which had their chromosomes counted.

TABLE III

CHROMOSOMES OF PROGENY OF TRIPLOID DATURA POLLINATED BY DIPLOID

Nos. and Assortment of Chromosomes..................	12 + 12	13 + 12	14 + 12 or 13 + 13	....	24 + 12 .. 18 + 18
Nos. of plants............	24	33	10	....	....
Calculated on random assortment for 4096 ovules.	1	12	66	etc......	....

The number of normal progeny shown in Table III is much beyond expectation (on the hypothesis that orientation of trivalents in the first division of the megaspore mother-cell is random), even if we allow the excessive total of over 4,000 ovules to 3 capsules. Detachment of chromosomes in the megaspore-mother-cells to the maximum extent found in the pollen-mother-cells will only partially account for this excess. Similar results were obtained by van Overeem with triploid *Œnothera biennis* pollinated by the normal (9).

Triploid Inheritance.—The 75 progeny showed triploid or trisomic (not disomic) inheritance (2) of two probably independent pairs of genes, those for purple and white flowers, and those for prickly and smooth capsules.

Distribution of Extra Chromosomes.—Among the 33 plants with one extra chromosome, cases were found where this extra chromosome was extra large, large, medium, small, or extra small. These plants showed 11 bivalents and 1 trivalent at the late prophase and early first metaphase. Ten different forms were recognized by external features among 30 of the 33 forms with an extra chromosome. (Three plants have not yet been identified.) Among these ten forms, 1 form (Globe) occurred 5 times, 3 forms (Buckling, Ilex, and Reduced) occurred 4 times, 2 forms (Glossy and Elongate) occurred 3 times, 3 forms (Rolled, Cocklebur, and Poinsettia) occurred twice, and 1 form (Microcarpic) occurred once. The expectations for each of 12 possible forms are presumably equal, namely 2.5. The Datura plants with 2 extra chromosomes so far examined showed 10 bivalents and 2 trivalents at the first prophase.

Thus the random assortment of chromosomes in triploid Daturas parallels the conclusions as to the random assortment of genes in triploid (trisomic) inheritance, and adds to the evidence for the chromosomal theory of heredity given by the cytological and genetic work on Drosophila (4) and other insects.

LITERATURE CITED

1. Belling, J. 1921. The Behavior of Homologous Chromosomes in a Triploid Canna. *Proc. Nat. Acad. of Science,* 7: 197–201.
2. Blakeslee, A. F. 1921. Types of Mutations and their Possible Significance in Evolution. Amer. Nat., 55: 254–267.
3. Blakeslee, A. F., J. Belling, and M. E. Farnham. 1920. Chromosomal Duplication and Mendelian Phenomena in Datura Mutants. *Science,* 52: 388–390.
4. Bridges, C. B. 1921. Triploid Intersexes in *Drosophila melanogaster. Science,* 44: 252–254.
5. Gates, R. R. 1909. The Behavior of Chromosomes in *Œnothera lata* × *gigas. Bot. Gaz.,* 48: 179–199.
6. Geerts, J. M. 1911. Cytologische Untersuchungen einiger Bastarde von *Œnothera gigas. Ber. d. Deutsch. Bot. Ges.,* 29: 160–166.
7. de Mol, W. E. 1921. Over het voorkomen van heteroploide varieteiten van *Hyacinthus orientalis* L. in de Hollandshe kulturen. *Genetika,* 3: 97–192.
8. Osawa, I. 1920. Cytological and Experimental Studies in Morus, with Special Reference to Triploid Mutants. *Bull. Imp. Sericult. Exp. Sta. Japan,* 1: 317–369.
9. van Overeem, C. 1921. Uber Formen mit abweichender Chromosomenzahl bei *Œnothera. Beih. z. Bot. Centralbl.,* B. 38, Abt. 1, Heft 1, S. 73–113.